

The effect of reintroductions on the genetic variability in Eurasian lynx populations: the cases of Bohemian–Bavarian and Vosges–Palatinian populations

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Received: 16 August 2015 / Accepted: 29 March 2016 / Published online: 4 April 2016
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Abstract Over the past ~40 years, several attempts were made to reintroduce Eurasian lynx to suitable habitat within their former distribution range in Western Europe. In general, limited numbers of individuals have been released to establish new populations. To evaluate the effects of reintroductions on the genetic status of lynx populations we used 12 microsatellite loci to study lynx populations in the Bohemian–Bavarian and Vosges–Palatinian forests. Compared with autochthonous lynx populations, these two reintroduced populations displayed reduced genetic diversity, particularly the Vosges–Palatinian population. Our genetic data provide further

evidence to support the status of ‘endangered’ and ‘critically endangered’ for the Bohemian–Bavarian and Vosges–Palatinian populations, respectively. Regarding conservation management, we highlight the need to limit poaching, and advocate additional translocations to bolster genetic variability.

Keywords Lynx · Microsatellites · Population history · Reintroduction

Introduction

The Eurasian lynx (*Lynx lynx* Linnaeus, 1758) is the largest European felid. Historically it existed throughout most of continental and Scandinavian Europe—a distribution that was substantially reduced by direct persecution as well as loss of habitat and prey (Breitenmoser 1998). Presently, populations exist in Western Europe with too few individuals to be considered self-sustaining; all of which were established through reintroduction efforts since the 1970s (Arx et al. 2009).

Due to their complexity (logistical, socio-economic, political), reintroductions usually involve the translocation of only a small number of individuals, not all of which will survive to become founders (e.g. Vandel et al. 2006). Thus, genetic variation in reintroduced populations may be reduced compared with the source population. Subsequent loss of variation through genetic drift, compounded by inbreeding, is to be expected in such small populations (e.g. Fickel et al. 2005). Poaching of lynx—a manifestation of the conflict between humans and lynx (e.g. Andrén et al. 2006; Breitenmoser and Breitenmoser-Würsten 2008; Breitenmoser et al. 2010; Lücktrath and Schraml 2015)—puts further strain on these genetically impoverished

Data accessibility: Microsatellite data were deposited in Dryad, doi:10.5061/dryad.9k3k5.

Electronic supplementary material The online version of this article (doi:10.1007/s10592-016-0839-0) contains supplementary material, which is available to authorized users.

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populations. A reduction in fitness due to low genetic variation and/or inbreeding has not yet been documented for wild lynx, but has been shown for captive lynx (Laikre 1999) that suffer problems similar to reintroduced populations (low diversity, few founders, inbreeding).

To date, only one study has published the genetic assessment of a reintroduced lynx population (Dinaric population: Sindičić et al. 2013). The authors reported low genetic diversity and significant inbreeding, and summarized their findings as “grim”. This study contradicts a previous ‘demographic assessment’ of the same population—i.e. from the viewpoint of population size and distribution over time—which had reported this reintroduction as “successful” (Arx et al. 2009). Such assessment discrepancies illustrate the need for an evaluation of the genetic status of reintroduced lynx populations in order to set appropriate genetics-based conservation goals (Frankham et al. 2010), and to provide an additional metric to monitor and to compare the development of reintroduced populations.

In light of this, we evaluated the genetic status of two reintroduced Eurasian lynx populations (Bohemian–Bavarian and Vosges–Palatinian; see Fig. 1a), and compared this with data for reintroduced and autochthonous European lynx populations of different demographic status. In this manner, we aimed to provide further genetic data to improve our understanding of the effect of establishing small, isolated populations of large carnivores by reintroduction.

Methods

The Bohemian–Bavarian (BB) population was founded by ‘unofficial’ introduction of 5–10 lynx of mostly unknown origin to Bavaria in the early 1970s (it included 3 + lynx from Slovakia; Festetics 1980; Wölfl et al. 2001), and later supplemented with individuals released on the Czech side of the BB Forest in 1982–1989 (18 lynx from Slovakia; Červený and Bufka 1996). The Vosges–Palatinian (VP) population was founded by 21 lynx released between 1983 and 1993, originating mostly from what are now Slovakia and the Czech Republic (Vandel et al. 2006).

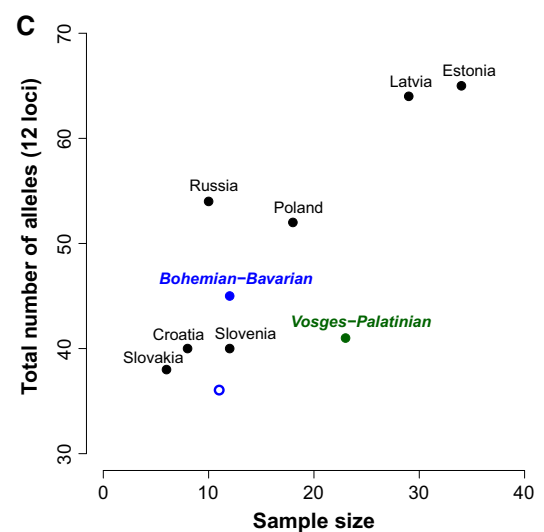
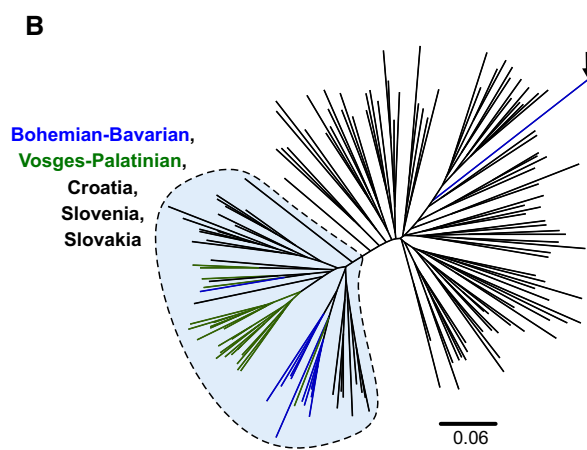
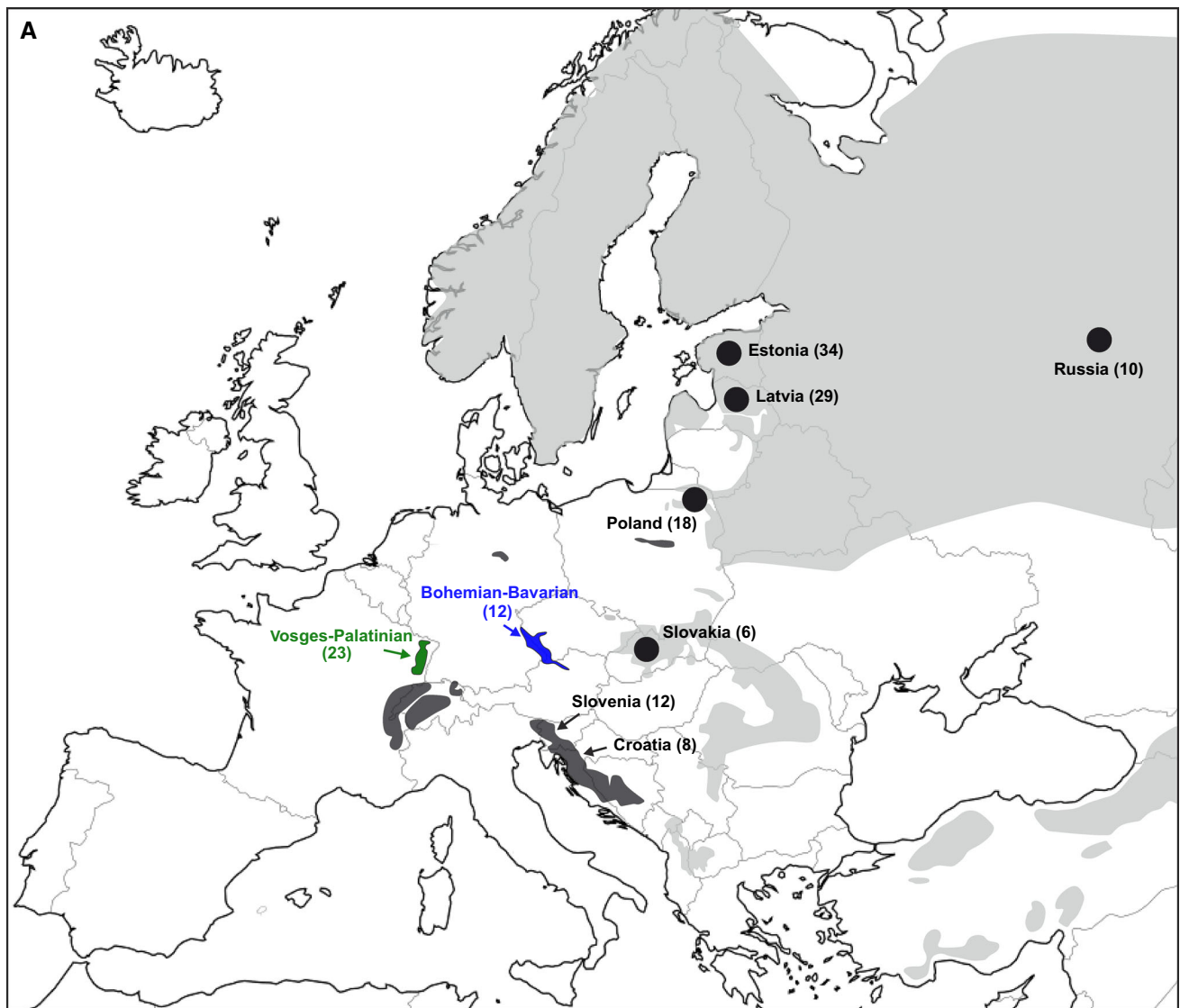
We obtained 130 non-invasively collected samples (scat) from the Bavarian portion of the BB population, 23 tissue samples from the Vosges portion of the VP population, and 117 tissue and/or blood samples from seven other Eurasian lynx populations (reintroduced: Croatia $n = 8$, Slovenia $n = 12$; autochthonous: Slovakia $n = 6$, Estonia $n = 34$, Latvia $n = 29$, Poland $n = 18$, Russia $n = 10$; Fig. 1a). DNA was extracted using a commercial kit (GEN-IAL GmbH, Troisdorf, Germany).

Fig. 1 a A map indicating the number and origin of lynx in study; larger occurrences are indicated (following IUCN red list data 2016): light grey for autochthonous populations, dark grey for reintroduced populations, blue and green for the Bohemian–Bavarian and Vosges–Palatinian populations, respectively. **b** An unrooted neighbour-joining tree based on the proportion of shared alleles ($1-P_S$) between multilocus microsatellite genotypes (following Bowcock et al. 1994). **c** The total number of alleles plotted against the total number of samples, by locality. The Bohemian–Bavarian and Vosges–Palatinian populations are highlighted in blue and green, respectively. The open blue circle represents the Bohemian–Bavarian population, excluding one admixed individual (see text)

We genotyped samples at 12 microsatellite loci designed for domestic cat (Menotti-Raymond et al. 1999, 2003) or Canadian lynx (Carmichael et al. 2000): F115, FCA441, FCA506, LCA110, FCA718, FCA006, FCA008, FCA082, FCA0097, FCA105, FCA229, FCA1023, following protocols in Schmidt et al. (2009).

Amplification success rate for scat samples (Bavarian) was 17.12 % (2–4 PCR replicates per sample). To avoid misleading results by allelic dropouts and false alleles, we followed the Maximum Likelihood approach (Miller et al. 2002) by genotyping each sample in parallel, not allowing for any allele mismatch between parallels. If a mismatch occurred, we discarded that sample and analysed two new parallels from a new DNA extraction of that sample. Genotypes were scored only if no mismatch occurred, otherwise the sample was discarded (we did not extract the sample a third time). In the end, thirty of the 130 scat samples were successfully genotyped at a sufficient number of loci (success rate = 88.9 %) to proceed with the identification of individuals (using CERVUS v.3.0, Kalinowski et al. 2007). Genotypes of scat samples were assigned to the same individual based on genotype similarity. Despite the conservative approach described above, some discrepancies between genotypes assigned to the same individual existed: (i) one case of large allele dropout, and (ii) two cases of allele-size shift (2 bp) due to stuttering. While we detected 18 unique individuals among the 30 scat samples, we proceeded with genetic analyses for only 12 of these lynx to reduce the amount of missing data in the dataset (only one missing locus permitted per sample).

For all analyses, sampling locations (countries) were defined as populations rather than using the occurrence-based definitions (Arx et al. 2004). None of the loci were at linkage disequilibrium in any of the populations tested (GENEPOP v.3.4, Raymond and Rousset 1995). We found no deviations from HWE; such deviations are potentially due to presence of null alleles, allelic dropout and/or false allele scoring due to stuttering (MICRO-CHECKER v.2.2.3; Oosterhout et al. 2004). F_{IS} was



calculated for each population using FSTAT v.2.9.3.2 (Goudet 2002). Several analyses were carried out in the statistical programming environment R (<http://www.cran.r-project.org/>): *Memgene* v.1.0 (Galpern et al. 2014) to determine the proportion of shared alleles among samples, calculated as $1 - P_S$, where P_S is the proportion of shared alleles (following Bowcock et al. 1994); *PopGenReport* v.2.1 (Adamack and Gruber 2014) for determining allelic richness (A_R) accounting for differences in sample size and genotyping success; and *PopGenKit* v.1.0 (Paquette 2012) for calculating observed (H_O) and expected heterozygosities (H_E).

Results and discussion

In order to place measures of genetic diversity of the reintroduced BB and VP populations in the context of their source of origin, we examined their genetic relationships to other populations using an individual-based multilocus approach (Bowcock et al. 1994). The unrooted neighbour-joining tree (Fig. 1b) shows that most individuals from the two target populations were more closely related to lynx from their known (for VP) or suspected (for BB) origins than to lynx from the other reference populations. For both BB and VP, individuals were found to cluster largely within distinct clades, while this was not observed for the Dinaric population (Croatia and Slovenia) and its founder, the Carpathian population (represented here by Slovakia): lynx from these populations were not distinguishable from each other in this analysis (black branches in highlighted portion of Fig. 1b).

One BB individual was genetically similar to lynx from Poland (indicated by the arrow in Fig. 1b). Two independent scat samples of this individual were genotyped, and these differed by only one locus (missing data). It is thus unlikely that the genetic similarity of this lynx to those in Poland stems from genotyping error(s) of the non-invasively collected samples. An assignment analysis using structure (Supplementary Material) suggests that this individual is admixed, with a high proportion (~60 %) of Polish ancestry. This implies successful interbreeding of local wild (BB) lynx with Polish lynx from an unknown source. The putative Polish ancestor(s) may represent natural long distance disperser(s), escapee(s) from an enclosure in the Bavarian Forest National Park (four of which escaped over the past 25 years), or undocumented/unofficial release(s) in or near the BB population.

Measures of genetic diversity (A_R , H_O , H_E , and F_{IS}) for lynx populations other than BB or VP (Table 1) corresponded well to those published elsewhere (Ratkiewicz et al. 2014; Sindičić et al. 2013; Schmidt et al. 2009; Rueness et al. 2003): (1) the autochthonous Baltic,

Table 1 Number of Eurasian lynx and genetic diversity measures

| Location | N | A_R | H_O | H_E | F_{IS} |
|--------------------------------|-----|-------|-------|-------|----------|
| Bohemia-Bavaria (BB) | 12 | 3.26 | 0.472 | 0.473 | 0.051 |
| Vosges-Palatinian (VP) | 23 | 2.79 | 0.454 | 0.474 | 0.068 |
| Other reintroduced populations | | | | | |
| Croatia | 8 | 3.33 | 0.510 | 0.511 | 0.068 |
| Slovenia | 12 | 3.04 | 0.490 | 0.511 | 0.088 |
| Autochthonous populations | | | | | |
| Slovakia | 6 | 3.16 | 0.639 | 0.523 | −0.133 |
| Estonia | 34 | 4.16 | 0.667 | 0.662 | 0.009 |
| Latvia | 29 | 4.28 | 0.652 | 0.682 | 0.062 |
| Poland | 18 | 3.71 | 0.616 | 0.601 | 0.004 |
| Russia | 10 | 4.37 | 0.717 | 0.700 | 0.029 |

Provided are the number of lynx (n), allelic richness (A_R), observed (H_O) and expected (H_E) heterozygosity, and the inbreeding coefficient (F_{IS})

A_R determined using rarefaction (sampling 8 random lynx per location, except for Slovakia)

Carpathian and Russian lynx populations had moderate-to-high diversity, and (2) the reintroduced Dinaric lynx population had lower diversity. In this context, the BB and VP lynx clearly displayed the low genetic diversity characteristics of other reintroduced lynx populations (Table 1).

Although our BB samples all originated from the Bavarian side of the BB ecosystem, we believe that our results are valid for the population as a whole, given that there is no barrier to dispersal (Magg et al. 2015). The measures of diversity for this population (Table 1; Fig. 1c) are very similar to those for the Dinaric population (Croatia & Slovenia), which has been aptly characterized as “grim” (Sindičić et al. 2013). Lynx of the BB population fare no better, and their ‘endangered’ status (Arx et al. 2004) is merited. Suitable habitat connecting BB to neighbouring populations (Carpathian) is available and ought to be maintained and enhanced to promote the influx of diversity into the BB population (Magg et al. 2015).

The VP population had the lowest diversity of all our study areas (Table 1; Fig. 1c). The total number of alleles ($N_A = 41$) among 23 VP samples is only one more than among 8 Croatian samples ($N_A = 40$), which themselves exhibit low variability. The low diversity in VP can probably be attributed to the low number of reproducing founders (estimated to be 4 females and 6 males *at best*; Vandel et al. 2006); absence of connectivity to other populations means that there is no opportunity for immigrants to bolster diversity and to replace potential losses. We concur with the assessment that the VP population should be regarded as critically endangered (Chapron et al. 2014).

Given their genetic status, both populations (especially VP) would benefit from an influx of genetic diversity by means of further reintroductions. The impact on variability following the introduction of individuals is illustrated by the admixed BB lynx (above); when this lynx is omitted from analysis, the amount of variation observed in this population is notably reduced (open and closed blue circles in Fig. 1c). In a long-term context, previous studies have shown that few individuals (immigrants/translocations) can suffice to significantly bolster variability in a population (Keller et al. 2001; Pimm et al. 2006; but see also Kenney et al. 2014); this is fortunate, as large home ranges and limited suitable habitat restricts the number of lynx that can feasibly be released successfully in these areas. For the BB and VP populations, we advise a small number of lynx originating from a portion of the Carpathian population other than Slovakia, which directly or indirectly already contributed most/all of their founding individuals. However, to determine which of these other Carpathian populations would be most suitable to supplement BB and VP requires further study. For BB, additional measures (including releases) to reinstate and maintain connectivity to neighbouring populations would also be highly beneficial (Müller et al. 2014; Magg et al. 2015).

A major obstacle in establishing and maintaining sustainable lynx populations in Europe is poaching (e.g. Breitenmoser 1998; Andrén et al. 2006; Breitenmoser and Breitenmoser-Würsten 2008; Breitenmoser et al. 2010). Lynx are protected under the EU Habitats Directive (Council Directive 92/43/EEC) since 1992, and their illegal killing is a criminal offense that may carry up to 5 years of imprisonment. However, enforcing the law is very challenging because perpetrators essentially need to be ‘caught in the act’ for conviction, for which government resources are sorely lacking or entirely missing. For this reason, dialogue and education of stakeholders (e.g. hunters, wildlife and forest managers, conservationists) is advocated, to identify and mitigate colliding interests and, ultimately, to reduce illegal killing of lynx (e.g. Breitenmoser et al. 2010; Lühtrath and Schraml 2015). While law enforcement in cases of poaching needs to be enhanced, addressing the social dimension of hunters’ opposition to lynx is also a priority. For both BB and VP, illegal killing represents the greatest threat to lynx, reducing their numbers and restricting their range to protected areas and their vicinity (Müller et al. 2014; Chapron et al. 2014; Wölfl et al. 2001). Low genetic diversity in these populations revealed by our study may further increase the threat for their survival. As we have illustrated above (Fig. 1c), the removal of a single individual (e.g. by poaching) can greatly impact the genepool in these small reintroduced populations.

Acknowledgments This research was made possible by a Leibniz Grant (SAW-2011-SGN-2) to DWF and JF, and a Grant to JKB by the Deutscher Akademischer Austauschdienst (A/11/93927). We are also grateful for the financial support of the Nationalparkverwaltung Bayerischer Wald. We gratefully thank M. Sindičić, P. Männil, J. Ozolins and the French Office National de la Chasse et de la Faune Sauvage (ONCFS) for providing samples. We would also like to thank two anonymous reviewers for their helpful comments. The license for lynx live-trapping and blood sampling in Poland was obtained from the National Ethics Committee for Animal Experiments (no. DB/KKE/PL—110/2001) and the Local Ethics Committee for Animal Experiments at the Medical University of Białystok, Poland (no. 52/2007). Import of samples from Russia was licensed by CITES permission no 12RU000512.

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